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**THE IMPORTANCE OF
RUNOFF AND WINTER ANOXIA
TO P AND N DYNAMICS
OF A BEAVER POND**

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THE IMPORTANCE OF RUNOFF AND WINTER ANOXIA
TO P AND N DYNAMICS OF A BEAVER POND

Report prepared by:

Kevin J. Devito*

Watershed Ecosystems Program, Trent University
P.O. Box 4800, Peterborough, Ontario, Canada K9J 7B8

and

Peter J. Dillon

Dorset Research Centre, Ontario Ministry of the Environment
Bellwood Acres Road, P.O. Box 39, Dorset, Ontario, Canada P0A 1E0

*Present address: Department of Geography, York University
North York, Ontario, Canada M3J 1P3

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ABSTRACT

A mass balance approach was used to determine the factors influencing phosphorus and nitrogen dynamics in beaver ponds. The relationships of runoff, pond surface water temperature, dissolved oxygen (DO) and redox potential (ORP) to the annual and seasonal total phosphorus (TP) and total nitrogen (TN) retention of a headwater beaver pond situated on the Precambrian Shield, central Ontario, were examined during 1987-88. Annual retention of TP (-11%) and TN (-5%) were low. P and N were transformed within the pond. On an annual basis inputs exceeded outputs of total reactive P (71%) and $\text{NO}_3\text{-N}$ (35%) and outputs exceeded inputs of total unreactive P (-33%) and total organic N (-26%), while inputs approximated outputs of $\text{NH}_4\text{-N}$ (-8%). Marked seasonal trends in P and N retention were observed. Trends in monthly TP and TN retention showed a strong inverse relationship with runoff. There was a weak relationship between monthly retention and average water temperature and ORP. The timing of the major processes of nutrient cycling with seasonal variations in runoff and nutrient transport influenced the seasonal, and thus annual, TP and TN retention. Positive monthly retention coincided with low runoff and high biotic assimilation during the growing season. Winter ice cover was associated with undetectable DO and low ORP (<0 mV) and increased levels of P and N, particularly $\text{NH}_4\text{-N}$ ($>800 \mu\text{g L}^{-1}$). High levels of P and N in the water were coupled with increased runoff and potentially low biotic assimilation resulting in a net release of TP and TN during the winter. Large flow-through of waterborne inputs and flushing of regenerated P and N from the beaver pond occurred during peak snowmelt runoff, resulting in low annual retention. Estimates of burial rates suggest that P and N have accumulated in the pond sediments.

Initial accumulation of flooded forest material and input of organic matter by beaver may be very important to the P and N dynamics of the pond, representing a long term source of nutrients to the pond water and outflow.

KEY WORDS: beaver pond, ice cover, nitrogen, nutrient retention, phosphorous, Precambrian Shield, runoff, water residence time, winter anoxia,

Topic Sentence:

- 1) Seasonal and annual phosphorous and nitrogen budgets of a beaver pond
- 2) The role of beaver ponds in P and N dynamics of headwater streams of the Precambrian shield
- 3) The role of hydrology in P and N dynamics of a beaver pond.
- 4) The role of winter anoxia in P and N dynamics of a beaver pond

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INTRODUCTION

Beaver (*Castor canadensis*) activity, such as dam-building and subsequent flooding of riparian zones can have a large influence on the hydrology and nutrient dynamics of streams within the local landscape (Dahm *et al.* 1987, Naiman and Melillo 1984, Parker 1986). Beaver ponds are positioned such that much of the runoff from a catchment must pass through them and therefore they can greatly influence the export and transformation of nutrients from terrestrial to down stream ecosystems (Naiman *et al.* 1987).

Despite the possible influence and relative abundance of beaver, our ability to generalize about P and N dynamics in beaver ponds is still limited. Sequestering of P and N in deposited sediments has been reported in mountain areas of Wyoming (Maret *et al.* 1987) and the Precambrian shield area of Quebec (Naiman and Melillo 1984). In contrast, Dodds and Castenholz (1988) report a large flow-through of N in a beaver inhabited spring pond in Oregon. Devito *et al.* (1989) report low retention of waterborne TP and TN in two beaver ponds on the Precambrian Shield of central Ontario. Devito *et al.* (1989) measured a net retention of inorganic N and net release of organic N, but analysis of the forms of P have not been done.

At present, no studies have looked at processes influencing P and N transport and mobilization in beaver ponds or other small wetlands. Previous work by Devito *et al.* (1989) suggests that seasonal variations in P and N may control annual and thus long term retention in beaver ponds on the Precambrian Shield. Annual retentions of TP and TN

were the difference between positive retention during the ice-free season and significant net output during the winter and spring. The seasonal budgets of other beaver ponds on the Precambrian Shield or other geographical regions are not known.

Both hydrologic and chemical processes are believed to influence nutrient export and cycling in streams and wetlands (e.g., Bayley *et al.* 1985, King 1985). Hydrology acts as a vehicle for export and the losses of dissolved and particulate substances have been related to the magnitude of runoff, water retention time and water flow pathways in both aquatic and terrestrial ecosystems (Gorham *et al.* 1979, Hill 1988, Bilby 1981). The hydrologic mobility of P and N may be controlled by homeostatic processes in the sediments and surface waters which limit or enhance the transfer of nutrients to the hydrologic component. The dominance of anoxic processes in regenerating nutrients and introducing them into the stream water has been observed in beaver dams and reservoirs (Dahm *et al.* 1987, Baxter 1977), but they have not been directly related to seasonal or annual retention of P and N within a stream reach. Knowledge of the interaction of hydrology and anoxic processes in beaver ponds and how these vary seasonally are necessary to develop an understanding and generalize about the nutrient dynamics in beaver ponds and the adjacent catchment.

We examine the influences of hydrology and water redox processes on phosphorus and nitrogen dynamics in a beaver pond situated on the Precambrian Shield. This quantitative information is needed to generalize about the possible role of beaver ponds on nutrient transport and retention in small headwater streams of the Precambrian Shield. The magnitude of runoff and water retention time of the pond were examined in relation to

annual and seasonal patterns of TP and TN export and retention. Physical and chemical parameters and nutrient concentrations of water in the pond were measured through the 1987/88 year to determine the relationship between redox potential, the form and availability of P and N and its influence on annual and seasonal retention of these nutrients.

STUDY AREA

The beaver pond (Hp4-bp) is located in Harp Lake subcatchment 4 (45° 23' N, 79° 08' W) which is situated near the southern border of the Precambrian Shield, in central Ontario, Canada (Fig. 1). The mean annual January and July air temperatures in the study area are -11.0 and 17.7 °C, respectively. The water bodies in this area are generally ice-covered from about the beginning of December to the middle of April. The area receives 900-1100 mm/yr of precipitation with 240-300 mm falling as snow. Each month during the period of snow and ice-cover some precipitation falls as rain. The long-term annual runoff is 400-600 mm/yr. A more detailed description of the climate and physiography, geology, and geochemistry of the area and at Harp 4 subcatchment has been reported by Scheider *et al.* (1983), McDonnell and Taylor (1987), and Devito *et al.* (1989).

The beaver pond (Hp4-bp) collects drainage from the upper reaches (61.5 ha) of the subcatchment (Fig. 1). It is a shallow (1.2 m average depth), steep-sided, dystrophic pond with floating mats of *Sphagnum* spp. and Labrador tea (*Ledum groenlandicum*) along the shore. The beavers flooded a low-lying forest and numerous dead tree snags still stand throughout much of the pond. A small valley bog (5m depth) was also flooded and a small

ring (0.59 ha) of floating *Sphagnum*, *L. groenlandicum*, and eastern larch (*Larix laricina*) remains in the centre of the pond.

There are several ephemeral channelized inflows into the pond. Hp4-15, Hp4-14 and Hp4-B drain moderately sloped uplands of primarily deciduous forests; the former contains a small beaver pond. The main perennial inflow, Hp4-18, drains a substantial portion of the watershed (39.2 ha) containing a large conifer swamp and a beaver pond. Unchannelized inputs derived from the area adjacent the pond (9.7 ha) drain moderate grade uplands of deciduous forests with small stands of conifers. The depth of overburden surrounding the beaver pond ranges from 1-2 m to exposed bedrock.

METHODS

Precipitation depths and air temperature data were obtained from a meteorological station located within 1 km of the pond (Locke and de Grosbois 1986). Streamflow at the mouth of Harp 4 subcatchment has been measured since 1976 (Scheider *et al.* 1983). Stream discharge at the beaver pond outflow, Hp4-13, was continuously monitored from May 1987, to June 1988. From March 1987 to June 1988 instantaneous discharges of the inflow streams to Hp4 beaver pond were measured at least once a week, but more frequently (often twice daily) during peak flow. Mean daily discharge data were calculated by linear integration of instantaneous discharge measurements (Scheider *et al.* 1979). Discharge at Hp4-18 was estimated by regression relationship between instantaneous discharge at Hp4-18 and that at Hp4-13:

$$\text{Discharge Hp4-18} = 0.557 * (\text{Discharge Hp4-13})^{1.03}, n=46, R^2=0.909, se=4.32$$

Runoff from ungauged areas adjacent the pond was estimated from the unit areal runoff at Hp4-13 during the study period. Water level in the pond was continuously monitored during the ice-free period of 1987 (Fig. 2). Staff gauge readings were recorded on a daily to weekly basis during the other periods.

Precipitation, stream and pond water sampling were carried out as described by Locke and Scott (1986). During 1987/88 samples were taken daily to weekly according to discharge. Surface water of Hp4 beaver pond was sampled at two depths, 0.3-0.5 m and 0.9-1.1 m below the water surface, at each of 4 sites in the pond (Fig. 2). During the winter, sampling was carried out through holes cut in the ice with plastic AVS collars frozen in place to prevent surface rain and meltwater draining into the underlying water column.

Analytical methods are reported in Table 1. The platinum/calomel electrode used for ORP measurements was standardized with Zobell solution (Zobell 1946). The calomel electrode potential (EM) was converted to the standard hydrogen potential (EH) and corrected for temperature (T) using the equation of Skoog and West (1976), where: $EH = EM + 223 + 0.76 T (^{\circ}C)$. Total organic nitrogen (TON) was calculated as $TKN - NH_4-N$, total unreactive P (TUP) as $TP - TRP$, and total nitrogen (TN) as $TKN + NO_3-N$.

Sediment cores were collected at the end of May in 1987 and 1988 (Fig. 2). A Plexiglass tube (10 cm diameter) was inserted by hand to approximately 20 cm depth into the

sediments and the extracted sediment was sectioned into 5 cm segments. Water content and bulk density were determined according to Paivanen (1969), and sediment TP and TKN as in Table 1.

Water and Nutrient Budget

A general water budget equation for the beaver pond is:

$$P + U_i + \sum^n S_i - E - S_o \pm \Delta W = 0 \pm e \quad (1)$$

All runoff from the base of each microcatchment was assumed to be surface stream flow. Inputs include stream inflows (S_i), precipitation depth (P) and ungauged runoff (U_i). Both subsurface and diffuse surface flow from ungauged areas adjacent to the pond were combined into ungauged runoff. Outputs include stream outflow (S_o), evapotranspiration (E) and change in storage (ΔW). For water storage, the change in volume of the pond was assumed to be constant with depth. Potential evapotranspiration (E) was estimated from Thornthwaite's (1948) equation. Deep ground water inputs and outputs were assumed to be negligible, due to the impermeable nature of the bedrock. The inputs should balance outputs \pm measurement errors (e). Chloride budgets were measured as a check on hydrologic budgets (Kadlec and Kadlec 1979).

For this study, waterborne nutrient retention (RT) was calculated from inputs which include bulk atmospheric deposition (P_i), stream inflow (S_i), unchannelized or ungauged inflows (U_i) and outputs as stream outflow (S_o):

$$\pm RT = P_i + \sum^n S_i + U_i - S_o \quad (2)$$

Both wet precipitation and dry deposition are incorporated into P_i .

Atmospheric deposition was calculated as described by Locke and de Grosbois (1986). Reactive phosphorus measurements in bulk deposition were previously determined to be $34\% \pm 50\%$ of the TP deposition (Dillon and Reid 1981).

Stream load was determined by integrating the estimated daily average discharge over each sampling period and multiplying the total volume of water by the nutrient concentration at the midpoint of each time interval (Scheider *et al.* 1979). Nutrient loads from adjacent ungauged areas (Ui) were determined from the mean monthly volume/weight concentration of three nearby upland streams multiplied by prorated monthly runoff volume. TN and TP storage in the sediments was estimated from the average chemical content multiplied by the estimated bulk density for each sediment subsample.

Absolute retention (RT) of the beaver pond was calculated as:

$$RT = (\text{total inputs} - \text{total outputs}) / \text{pond area},$$

Percent retention (%RT) as:

$$\%RT = ((\text{total inputs} - \text{total outputs}) / \text{total inputs}) * 100.$$

Error Estimates

The variance of water budget calculations was calculated to obtain the standard deviation (Winter 1981):

$$S_P^2 + S_U^2 + \Sigma^n S_i^2 + S_E^2 + S_{SO}^2 + S_{\Delta W}^2 = S_T^2 \quad (3)$$

where n equals the number of inflow streams (S_i) and S_T is the standard deviation of the

total monthly water budget. All the measurement errors are assumed to be independent and covariance terms are not included (Winter 1981). To obtain S_T^2 , total monthly water volumes were multiplied by their associated fractional error (C.V.) and then squared and summed. The variances of all products in this study were approximated as (Mood *et al.* 1974):

$$\text{VAR}(X,Y) = u_x^2 \cdot \text{VAR}(Y) + u_y^2 \cdot \text{VAR}(X) + \text{VAR}(Y)\text{VAR}(X) \quad (4)$$

$\text{VAR}(X)$ and $\text{VAR}(Y)$ are the product of the water volume or concentration multiplied by the fraction error (C.V.) and then squared. S_T^2 for each of the nutrient retention estimates was calculated using Eq. 3. To obtain S_T^2 for TN, TON, TIN and TUP retention, variance estimates associated with the parameters used to calculate each mass were summed. The variance associated with nutrient mass was determined for each sampling time interval and summed to produce either seasonal or annual values.

Error associated with daily and monthly stream discharge measurements are reported in Devito and Dillon (1992) and range from 18 - 73% for mean daily stream discharge. Based on a comparison of monthly stream discharge from several microcatchments in the study area the percent error in estimating monthly discharge volume by linear integrations is estimated at $\pm 27\%$ (Devito and Dillon 1992). Errors associated with measuring precipitation were not determined directly. Errors based on equipment used and the rain fall patterns in this area are assumed to be $\pm 21\%$ per month (see Devito *et al.* 1989, Winter 1981). The range of uncertainty for determining stage for the pond was ± 2 mm. The C.V. associated with estimating the area of the pond from airphotos are assumed to be $\pm 10\%$.

Analytical and sampling errors associated with determining stream water and bulk deposition chemistry of discrete samples ranged from 1.5% to 18% and are reported in Locke (1988) and Devito (1989). Errors associated with volume weighted concentrations are assumed equivalent to analytical and sampling errors.

The errors associated with each component of the budgets were assumed to be random and normally distributed. Potentially important unmeasured and systematic errors have not been included in the error analyses. The following variance estimates, therefore, must be considered as only the precision of water and nutrient budget estimates, and actual errors are probably greater than indicated (Devito and Dillon 1992).

RESULTS

Water and Waterborne Nutrient Budgets

Annual inputs and outputs of water and chloride for 1987/88 in Hp4-bp roughly balanced (Table 2). On an annual basis the major input was via runoff with precipitation contributing <15%. Potential rates of ET and change in storage were minor outputs representing <10 and <1% respectively. The relative contribution of each component varied seasonally. Positive retention of water and Cl occurred during the summer and winter with negative retention occurring during the spring (Table 2). Precipitation, potential ET and change in storage were dominant components of the summer budget. Runoff increased in

importance and represented the major input and output during the winter and spring months.

The chemical budgets strongly suggest that the pond has very low TP and TN retention efficiencies with absolute retentions less than the budget uncertainties (Tables 3 and 4). During the 1987/88 water year, there was a positive retention of TRP (71%) and negative retention of TUP (-33%), resulting in a low retention efficiency of TP (-11% or -12.1 ± 10.5 mg/m²). There was no significant retention of NH₄-N (-8%), but NO₃-N (35%) was retained in the pond. A net release of TON (-26%) resulted in a low retention efficiency (-5%) of 0.20 ± 0.19 g/m TN.

Marked seasonal trends in P and N retention were observed in Hp4-bp during 1987/88 (Tables 3 and 4). Generally P and N were retained during the summer months and released during the winter and spring. Relative retention of TUP and TON was variable with the greatest negative percent retention occurring during the winter. TRP and NO₃-N were exceptions. NO₃ was retained during all seasons except during spring where inputs approximated outputs. Relative retention of TRP was high in all seasons with an increase in absolute retention with an increase in inputs.

The absolute input and output of nutrients varied seasonally, with the greatest flux of P and N occurring via runoff during the winter and spring (Table 5). During April 1988, 29 to 35% of the annual input and output of TP and TN of Hp4-bp occurred.

Pond Hydrology and Chemistry

The outflow hydrograph and pond water levels from March 1987 to May 1988 are shown in Fig. 3. Discharge varied over the year, with low base flow through the summer and peak discharge during snowmelt in March and April. Discharge peaks occurring through late fall and winter were a result of snowmelt, associated with rain, where much of the accumulated snow pack was lost.

Water levels in the pond varied seasonally with runoff rates. The lowest water levels were observed during late summer. The potential water storage in the pond was small. A 20 cm rise during the fall represented only about 2 cm of runoff from the surrounding catchment. Water levels in the pond responded rapidly to increases in runoff with peaks in water level coinciding with outflow hydrographs (Fig. 3). Water levels exceeded the main dam height during both the 1987 and 1988 spring snow melt. The annual residence time of water for 1987/88 in the existing pond was 47 days (Table 5). This compares with 6 hours for the initial stream if it had the same channel structure as the outflow. The residence time of water varied seasonally, being 242 days for summer/fall and 26 days for winter/spring. During peak spring melt, April 7 1988, the residence time of water in the pond was less than 1 day.

Water temperatures of the pond varied seasonally from near 0°C in late winter to 30°C in mid summer (Fig. 3). There was little or no thermal stratification of the pond water through the ice free season. Thermal stratification began with ice formation and was maintained

through the winter until peak spring discharge and break up of the ice. The ORP and DO concentrations of both the surface and bottom water were generally high throughout the ice free season (Fig. 4), with DO concentrations periodically dropping below detection in the bottom water. The bottom water became anoxic following winter ice cover. The DO concentrations in the surface water (just below the ice) declined during the ice cover period. The entire water column became anoxic by late March, just prior to the spring melt.

Temporal and depth variations in P and N concentrations were related to periods of ice cover and thermal stratification (Figures 5 and 6). TP and TN concentrations were slightly higher during the summer, while minimum TN and TP concentrations occurred after increased runoff during the fall and spring. Concentrations near the surface generally remained low through the winter. The concentrations increased in the bottom water to near maximum annual values during early spring when highly anoxic conditions existed. TON and TUP were the predominant forms of N and P, with $\text{NH}_4\text{-N}$ and TRP contributing significant amounts to the bottom water during the winter. Inorganic N and TRP remained near detection limits throughout the ice free season. TRP concentrations increased in the bottom during winter anoxic conditions. High $\text{NO}_3\text{-N}$ concentrations occurred in the surface water during periods of snow melt and increased discharge. High levels of $\text{NH}_4\text{-N}$ ($>500 \mu\text{g L}^{-1}$) were observed in the bottom and eventually the surface waters in the beaver pond during the winter and early spring. Following spring snowmelt, concentrations in the water column were at or near minimum annual values.

Monthly Retention in Relation to ORP and Discharge

There is a strong inverse relationship between monthly retention of TP and TN and discharge in the beaver pond (Figures 7 and 8). Some of the scatter in the discharge vs RT relationship may be due to interaction with temperature and redox condition of the pond water. There is a weak relationship between monthly retention and average water temperature. Low average monthly ORP was associated with negative retention of TP and TN in Hp4-bp during the winter months. There are four months with average ORP near or below 200mV in which TP and TN retention is much less than ice-free months with similar or greater discharge. The lowest monthly retention for Hp4-bp occurred during December 1987 and March 1987 for TP and TN, respectively. The runoff volume during these months was less than half the maximum observed monthly runoff over the past 4 years.

Sediment P and N Content and Burial

The quantities of TP and TN in the top 15 cm of sediment in Hp4-bp are shown in Table 6. From core samples, the old forest floor was readily distinguishable by the presence of litter, forest mosses and upland soil horizons. Typically, 7 to 12 cm of sediment had been laid down at the coring sites since the pond was established. Information from air photos shows the pond being formed between 1960 and 1969. Based on an accumulation period of 20 to 27 years, a net annual burial rate of 0.15 to 0.55 g P m⁻² yr⁻¹ and 2.5 to 6.6 g N m⁻² yr⁻¹ was estimated from P and N content of sediment (including forest litter) above the forest floor (Table 6).

DISCUSSION

Annual P and N Retention

Low annual TP and TN retention in Hp4-bp appears to be a relatively long term phenomenon, as no significant retention was observed over 5 years, from 1983/84 to 1987/88, (Devito *et al.* 1989, Devito 1989). P and N mass balances for Hp4-bp appear to contradict the limited published data on beaver ponds (Naiman and Melillo 1984, Maret *et al.* 1987). Reduction in phosphorus and organic material has also been reported in water below retention reservoirs and in stream debris dams (Schreiber *et al.* 1981, Bilby 1981, Naiman *et al.* 1986). How then may the results from this study be extrapolated to other ponds in the southern Shield area and other geographical regions?

The influence of Hp4-bp on waterborne N retention appears to be similar to beaver ponds on the Precambrian Shield in Quebec studied by Naiman and Melillo (1984). Although they report a net accumulation, the majority of N (~95% of the inputs) passed through the beaver pond complexes. Considering the inherent uncertainties in the estimates, no retention of waterborne TN was detected. Accumulation of N in the pond sediments was attributed primarily to nitrogen-fixation in the sediments (Francis *et al.* 1985). Low waterborne retention but large sediment standing stock of N is similar to the situation observed for Hp4-bp.

Maret *et al.* (1987) reported a positive retention of TP, NO₃ and TKN during the ice-free season in a beaver pond complex in SE Wyoming. However, nutrient retention was highly

correlated with retention of suspended sediments. Beaver dams, and debris dams in general, have been reported to reduce fluvial erosion and increase retention of nutrients associated with organic and mineral sediments by moderating potential stream gradient (Parker 1986, Bilby 1981, Schreiber *et al.* 1981). Sediment loads of streams and fluvial erosion are of minor importance in the relatively low gradient, headwater streams on the Shield, even during peak snow melt (personal observation). The retentive function of beaver ponds may be greater in high gradient systems with large mineral sediment loads where construction of a dam results in deposition of that stream load (Parker 1986). Maret *et al.* (1987) found that the beaver pond did not reduce nutrient levels during the summer when particulate load and deposition were reduced. Bilby (1981) reports that debris dams were less efficient at retaining nutrients during conditions of minimum particulate transport.

Given the strong seasonal variation in retention, the period of measurement may also be important. The beaver pond studies mentioned previously were only conducted during the ice free period, and in this period the Hp4-bp pond efficiently retained P and N. The largest export of P and N occurred during ice cover in the winter and early spring. This implies that estimates of annual budgets must include continuous monitoring through all seasons rather than be based on extrapolations from measurements made in some seasons only.

It appears that Hp4 beaver pond primarily functions to transform inorganic forms of N and P into organic forms which are transported downstream. Transformation of waterborne inorganic forms of P and N to organic forms has been suggested in several geographically

diverse stream and riparian wetland ecosystems (Meyer *et al.* 1981, Triska *et al.* 1984, Kemp and Day 1984, Elder 1985).

Influence of Hydrology and Winter Anoxia on P and N Retention

Seasonal patterns of nutrient retention have been reported for many different wetland types (van der Valk *et al.* 1978, Klopatek 1978) but have not been reported for beaver ponds. The seasonal, and thus annual, retention in Hp4-bp is primary controlled by 1) the magnitude of runoff and the residence time of water in the beaver pond; and 2) regeneration of P and N via decomposition and/or leaching of organic sediments which buffers the dilution of outflow concentrations by increased discharge. The relatively long period of winter anoxia plays a key role in regeneration of P and N and making these nutrients available for hydrologic transport.

It is apparent from the data that gross export and absolute retention of P and N within Hp4-bp are strongly influenced by large seasonal variations in runoff. The hydrology is the primary vector of transport for P and N in this beaver pond. Seasonal discharge varied over four orders of magnitude while outflow concentrations remained almost constant; thus, P and N export was directly proportional to stream discharge. Runoff magnitude greatly influences the P and N dynamics because the velocity and residence time of runoff govern both the rate of nutrient uptake by various components and the magnitude of flowthrough and flushing of nutrients (Howard-Williams 1985, Baxter 1977). Marked seasonal variations in runoff are characteristic of temperate and boreal regions and increased gross export and

reduced retention of elements with discharge, primarily during snowmelt, has been reported in many streams and wetlands (Hill 1988, Meyer *et al.* 1981, Elder 1985, Pierson 1983).

The presence of a beaver pond is associated with large alterations in stream hydrology (Parker 1986). Construction of the Hp4-bp dam resulted in 2 orders magnitude increase in the annual residence time of water within the stream reach assuming the original channel had the same structure as the outflow. This may greatly increase the autotrophy in low order streams (Naiman *et al.* 1987) and greatly increase nutrient retention within the stream reach, as suggested by other work on debris dams (Bilby 1981, Naiman *et al.* 1987). However, an important consideration is the timing of the major processes of nutrient cycling with seasonal variations in runoff and nutrient transport (Hill 1988). Biotic assimilation appears to exert some control on P and N retention in the beaver pond during periods of low flow when potential water retention and residence times are high. However, these periods of high assimilation occur when nutrient transport is low and contribute little to the annual nutrient flux. Throughout the winter and spring, increased runoff, coupled with limited pond storage, greatly reduces the water residence time. Short residence time together with low temperatures further limits the influence of ecosystem production on surface water concentrations. Thus, it appears that a large portion of the annual P and N input may rapidly bypass biological and abiotic cycling. About 90 percent of the annual runoff and 80 percent of the annual P and N inputs and outputs to the pond occurred during the winter and spring resulting in large through-flow of nutrients and thus low annual retention efficiencies.

Episodic events are extremely important in the annual rates of P and N transport in to the study beaver pond. Accumulation of precipitation within a snow pack redistributes several months' precipitation into one or a few hydrologic events. Greater than 40% of the annual input and output in 1987/88 occurred in 4 separate winter and spring events. Estimated residence time in Hp4-bp during peak snow melt was less than one day and removal of nutrients from the water column would be restricted to instantaneous reactions. Greater than 50% of the annual water and nutrient yield from many temperate and boreal watersheds has also been reported to occur during episodic storms or snow melt (Meyer *et al.* 1981, Pierson 1983, Scheider *et al.* 1983, Schindler *et al.* 1976).

Inorganic forms of N and P were efficiently retained within the pond through the year, suggesting rapid assimilation into a component which is independent of runoff magnitude. Microbes and algae have been shown to rapidly assimilate nutrients and may limit the amount of available (non-refractory) P and N in the water (Davis and van der Valk 1983, Warwick and Hill 1988) and may control short term storage and transport of inorganic P and N in freshwater wetlands (Richardson and Marshall 1986). This may occur underneath ice (Knowles and Lean 1987) or at times when plants are dormant and hydrologic fluxes high (Atchue *et al.* 1983). Intense competition for inputs and regenerated N and P by the microbial community may partly explain the efficient retention and transformation of TRP and $\text{NO}_3\text{-N}$ and the predominance of TUP and TON in the pond water of Hp4-bp. Microorganisms are readily transported in surface waters (Richardson and Marshall 1986). Thus microbial TP and TN storage would be influenced by the magnitude of runoff and

hydraulic retention times and may explain the high flowthrough rates of TP and TN in the study beaver pond.

The low annual retention in the study wetlands suggests that a large part of the P and N assimilated during the growing season is temporary. Although submergent macrophytes and associated epiphytes in the pond may be very important in removing P and N directly from the water, a large portion of assimilated nutrients is lost to the water column in the fall and winter following senescence (Davis and van der Valk 1983, Atchue *et al.* 1983). Translocation of nutrients from sediments by submergent vegetation can also function in effectively recycling nutrients from the sediments to surface waters, further limiting nutrient conservation by vegetation (Richardson and Marshall 1986).

Significant amounts of P and N may be regenerated from the accumulated organic matter in the pond sediments. Increased concentrations of DOC are associated with organic decomposition (Naiman *et al.* 1986), and were observed during the summer and winter in Hp4-bp (unpubl. data). Significant regeneration of P and N tied up in organic matter primarily by microbial mineralization of organic matter and indirectly through anoxic processes, has been measured in beaver ponds (Dahm *et al.* 1987) and other types of wetlands (Bayley *et al.* 1985, Richardson and Marshall 1986).

Anaerobic conditions in Hp4-bp during winter ice cover had a strong influence on the regeneration and concentration of P and N in the pond water and outflow. Similar regeneration of $\text{NH}_4\text{-N}$ and TP into the surface waters of small lakes from the water column

and sediments following anoxia induced by decomposition of organic matter during ice cover and thermal stratification has been reported in many water bodies in temperate and boreal regions (Carignan and Lean 1991, Mathias and Barcia 1980, Knowles and Lean 1987). A buildup of reduced forms of N and P in Hp4-bp surface waters resulted in disproportionately greater export of $\text{NH}_4\text{-N}$ relative to runoff and a negative storage of $\text{NH}_4\text{-N}$, as well as TP, during the winter and early spring. Flushing of nutrients from the pond was evident by the rapid reduction of P and N concentrations in the water column during spring melt in 1987 and 1988.

Oxygenated surface water persisted through much of the winter. Significant amounts of NH_4 and NO_3 may be consumed under ice by nitrification and denitrification and lost to the system as NO_2 or N_2 gas (Knowles and Lean 1987). However, nitrification as well as other microbial respiration processes may also contribute to the observed oxygen depletion in the surface waters and inhibit NH_4 oxidation during ice cover. The maintenance of reduced conditions which extend to the top of the water column in a shallow pond may greatly limit the loss of gaseous N and result in greater stream output of regenerated N. Existence of an oxygenated layer below the ice would be controlled by the magnitude and periodicity of runoff into the pond.

Large exports of $\text{NH}_4\text{-N}$ from Hp4-bp as well as other ponds in the study area (Devito *et al.* 1989) have occurred during the winter over several years, suggesting that the occurrence of highly reduced conditions in ponds is common in this area of central Ontario. High concentrations of NH_4 were observed in fall and winter below a beaver pond in the

Adirondack region of New York (Driscoll *et al.* 1987). Reduced forms of P and N may be characteristic of control structures on streams (Dahm *et al.* 1987) and marshes during their ice cover period (Lee *et al.* 1975, Klopatek 1978). Alteration of stream hydrology by a dam facilitates anaerobic conditions of the stream reach. Neither the inflow or outflow stream at Hp4-bp became anoxic (unpubl. data). The dam results in a dramatic increase in water depth and reduction in water velocity necessary for ice formation. Solid ice cover forms an efficient barrier to atmospheric oxygen and eliminates wind induced mixing which occurs during the ice free period. This barrier, combined with increased water residence time, results in a greater potential for oxygen depletion and the build up of reduced forms of P and N. Isolation and limited mixing of oxygenated cold, low density stream inflows with deeper pond water as a result of inverse thermal stratification under ice (Bergmann and Welch 1985) would further maintain anoxic conditions through out the winter.

Sediment Burial

The burial rates for Hp4-bp are slightly lower but comparable to burial rates of $26 \text{ g N m}^{-2} \text{ yr}^{-1}$ and $7 \text{ g N m}^{-2} \text{ yr}^{-1}$ reported for a beaver inhabited spring, in Oregon, and a beaver pond complex in Quebec (Dodds and Castenholz 1988, Naiman and Melillo 1984). No P accumulation rates in beaver ponds have been reported. Although there are large uncertainties associated with the burial estimates, long term sequestering of P and N is suggested. This contradicts the waterborne budgets for 1987/88. The paradox between the waterborne budgets and the large calculated sediment accumulation rate may be due to either budget errors or unmeasured inputs not directly linked to hydrology.

Errors associated with water and chemical budgets are so infrequently reported that it is difficult to determine if the errors associated with each component in this study are reasonable. The errors for annual estimates of stream nutrient flux in Hp4-bp ranged from 2 to 11%, with most SD near 10%. Elder (1985) reported similar errors of annual yield estimates for the Apalachicola River wetland system, calculated from the sums of squared component SD, of 5-6% for N and 8-9% for P. Dodds and Castenholz (1988) report means and ranges of estimates for a N budget of a pond and the resulting error estimates were much larger than calculated in this study. The errors associated with the water budgets of Hp4-bp seem reasonable, although perhaps small (see Devito and Dillon 1992). At 95 % confidence, residual errors represent approximately $\pm 20\%$ of the inputs. The burial rates are an order of magnitude greater than the budget error estimates suggesting that the large standing stock of P and N in the sediments must be derived from unmeasured inputs.

Groundwater may contribute significantly to the residual of the hydrologic and nutrient budget but was not measured. Using unit areal runoff estimates for the ungauged areas and neglecting deep groundwater fluxes still resulted in a relatively good balance of water and Cl. This fact and results of other studies by Scheider *et al.* (1983) and McDonnell and Taylor (1987) in Harp 4 subcatchment suggest that deep ground water fluxes are limited. The greatest unknown inputs originate from areas adjacent the pond. Ungauged inputs to Hp4-bp represented less than 10% of the total inputs limiting the error. Estimates of unit runoff and chemical concentration from small upland streams adjacent the pond appear to give reasonable estimates of nutrient yield (Devito and Dillon 1992).

There are several other possible sources which were not measured. Construction of a dam greatly increases the area of flooded soils. Rates of N-fixation in similar sediments, based primarily on the ice free season, range from 0.4 to 6.0 gNm⁻²/yr⁻¹ and approximate the net burial rates in Hp4-bp (Francis 1985, Dodds and Castenholz 1988, Howarth *et al.* 1988). However, these rates would vary seasonally and measured rates of denitrification for temperate and subarctic streams, ponds and lakes are well within the rates of N-fixation (Dodds and Castenholz 1988, Seitzinger 1988). There are no analogous microbial activities which could account for the large accumulation of P. Litter inputs from vegetation adjacent the pond have been reported to contribute very little to the P and N budget of beaver ponds and probably could not account for the large burial (Naiman and Melillo 1984, Dodds and Castenholz, Devito *et al.* 1989).

It is important to recognize the dynamic nature of beaver ponds and the beavers' influence on the landscape. Large initial input from forest litter and vegetation would have occurred as the beaver flooded the forested valley. Anoxic conditions in the sediments may slow decomposition and a considerable amount of the initially large pool of P and N may still remain. This together with leaching of P and N from old forest floor and weathering of flooded secondary minerals may result in the large P and N pool and an overestimation of the long term burial rates. In addition, beaver can actively transport large amounts of material and this can represent an important input from the adjacent upland into the pond sediments and stream (Dodds and Castenholz 1988, Naiman and Melillo 1984).

It is apparent that construction of a dam and beaver activity greatly increase the amount of organic and mineral materials which are hydrologically linked to the outflow stream (Naiman *et al.* 1987). This "reservoir" of P and N may be mobilized representing a low rate but long term source of nutrients to the pond water and downstream locations (Baxter 1977).

CONCLUSION

The results presented here help to clarify the relative importance of beaver ponds to the water chemistry of small headwater streams of the Precambrian Shield. Beaver ponds are not efficient at retaining waterborne TP and TN within a stream reach on an annual basis. Because of the large throughput of water and dissolved material, absolute rates of retention may be difficult to detect due to inherent uncertainties of the budgets. The need for error estimates is paramount in interpretation of budget residuals and is stressed in this study.

The magnitude of runoff and water residence time within the pond had the greatest influence on seasonal export and retention of TP and TN. As a consequence, limited retention of nutrients may occur in small beaver dams in regions with little stream sediment yield and especially during high flows (Baxter 1977). The low annual retention of nutrients in the beaver pond may be representative of other small headwater wetlands in the Precambrian Shield which are centrally located in catchment depressions and receive large flowthrough of water and nutrients from the surrounding uplands.

The hydrologic, geochemical and biotic processes interact in complex ways as biotic and geochemical cycling vary seasonally with the time and magnitude of water and nutrient transport. Most studies have focused on the physical effects of debris dams on water velocity and physical retention in a reach (Bilby 1981, Maret *et al.* 1987, Naiman *et al.* 1986); however, construction of Hp4-bp dam created the hydrological conditions for ice cover and long periods of anoxia which were important in the seasonal and annual P and N dynamics of the stream reach. Since beaver ponds may be important areas for trapping and processing organic matter, more work should focus on the importance of these areas for nutrient regeneration and introduction into streams (Dahm *et al.* 1987). The winter period of high respiration and organic matter oxidation relative to primary production is always followed by extreme runoff conditions during snowmelt. The hydraulic characteristics of the beaver pond are such that most of the incoming P and N and that accumulated in the surface waters are flushed from the system, resulting in a net efflux during the spring and low annual retention of P and N.

From a landscape perspective, greater export of nutrients via runoff to downstream ecosystems may occur in headwater catchments with beaver ponds than unaltered catchments. Burial rates suggest that P and N accumulated in Hp4-bp. Other unmeasured fluxes, such as initial accumulation of flooded forest material and input of organic matter by beaver, may be very important to the overall P and N flux of beaver ponds. Similar to the increased rates of organic matter export in beaver influenced streams in Quebec (Naiman *et al.* 1986), construction of the dam greatly increases the wetted area and thus

increases the mass of organic matter in contact with water and accessible to transport downstream.

From a stream ecosystem perspective, little P and N retention may occur in beaver ponds. The primary role of beaver ponds may be to transform P and N, reducing the flux of inorganic nutrients with a concomitant increase in organic nutrients to downstream ecosystems. Microbial or algal populations which are susceptible to hydrologic transport may provide a mechanism which results in flowthrough of inorganic nutrients in systems with low water retention and seasonally high ecosystem flushing. Low order streams in the Precambrian Shield are consistently interrupted by complex channel structures, such as beaver dams, which may alter the hydrology and redox environments. This study, along with the work of Naiman *et al.* (1986, 1987), provides more evidence to recognize the role of beaver in current concepts of stream ecosystem organization and stability such as the river continuum concept (Vannote *et al.* 1980) and nutrient spiralling (Elwood *et al.* 1983).

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TABLE 1 Analytical Procedures

Parameter	Abbreviation	Units	Procedure+
<u>Water Parameters</u>			
1 Total phosphorus	TP	$\mu\text{g/L as P}$	Acid digestion, acid molybdate colorimetry
3 Total reactive phosphorus	TRP	$\mu\text{g/L as P}$	Acid molybdate colorimetry*
1 Ammonium	$\text{NH}_4\text{-N}$	$\mu\text{g/L as N}$	Phenate - Hypochlorite colorimetry
1 Nitrite/nitrate	$\text{NO}_3\text{-N}$	$\mu\text{g/L as N}$	Hydrozine reduction - Azo dye colorimetry
2 Total Kjeldahl nitrogen	TKN	$\mu\text{g/L as N}$	Acid digestion - neutralization nitrogen and colorimetry
2 Chloride	Cl	mg/L	Thiocyanate colorimetry
3 Dissolved Oxygen	DO	mg/L	Winkler method
3 Redox potential	ORP	mV	Platinum/columel electrode@
<u>Sediment Parameters</u>			
2 Total phosphorus			Acid digestion - neutralization, acid molybdate colorimetry
2 Total nitrogen			Acid digestion - neutralization, colorimetry

1 OME laboratory, Dorset

2 OME laboratory, Rexdale

3 By the author, Dorset

+ Reference OME (1981)

* Modified from Stanton et al. (1977)

@ Skoog and West (1976)

TABLE 2 Seasonal and annual water (mm) and chloride (mg/m²) balance for Harp 4 beaver pond for the 1987/88 hydrologic year, ± 1 SD. A negative balance represents inputs < outputs, and a positive value represents inputs > outputs.

	Input			Output		Evapotranspiration	
	Stream Flow	Ungauged Flow	Precipitation	Stream Flow	Change in Storage	Balance (In-Out)	Thornthwaite
Harp 4 Beaver Pond							
<u>Water</u>							
summer	66 \pm 7	1 \pm 0	182 \pm 22	109 \pm 3	-90 \pm 24	230 \pm 33	275
fall	449 \pm 46	25 \pm 8	235 \pm 30	645 \pm 18	+96 \pm 25	-32 \pm 63	100
winter	1547 \pm 124	212 \pm 64	301 \pm 37	2032 \pm 48	-96 \pm 25	124 \pm 154	0
spring	3890 \pm 379	825 \pm 245	205 \pm 25	4894 \pm 142	+124 \pm 33	-98 \pm 475	86
annual	5952 \pm 401	1063 \pm 253	923 \pm 58	7680 \pm 151	+34 \pm 12	224 \pm 504	461
<u>Chloride</u>							
summer	0.04 \pm 0.01	<0.01 \pm <0.01	0.03 \pm <0.01	0.04 \pm <0.01	-	0.02 \pm 0.01	
fall	0.31 \pm 0.04	0.01 \pm 0.01	0.05 \pm 0.01	0.19 \pm 0.01	-	0.18 \pm 0.04	
winter	1.08 \pm 0.10	0.12 \pm 0.05	0.08 \pm 0.01	1.24 \pm 0.07	-	0.04 \pm 0.13	
spring	1.63 \pm 0.18	0.33 \pm 0.12	0.04 \pm 0.01	2.24 \pm 0.14	-	-0.24 \pm 0.26*	
annual	3.06 \pm 0.20	0.46 \pm 0.13	0.2 \pm 0.02	3.71 \pm 0.16	-	<0.01 \pm 0.29	

TABLE 3 Waterborne phosphorus input, output and retention (mgP/m²) for the 1987/88 hydrologic year for the Harp 4 beaver pond. Shown are estimates \pm SD.

Phosphorus Form	Input				Output		Retention	
	Stream Flow	Ungauged Flow	Precipitation	Total	Stream Flow	Absolute (In-Out)	Relative %	
<u>TRP</u>								
summer	1.8 \pm 0.2	0.0 \pm 0.0	1.8 \pm 0.7	3.6 \pm 0.7	0.5 \pm < 0.1	3.1 \pm 0.7	86	
fall	1.2 \pm 0.2	<0.1 \pm < 0.1	1.2 \pm 0.4	2.5 \pm 0.5	0.6 \pm 0.1	1.8 \pm 0.5	72	
winter	5.5 \pm 1.0	0.2 \pm 0.1	0.9 \pm 0.3	6.6 \pm 1.0	2.0 \pm 0.3	4.6 \pm 1.1	70	
spring	9.7 \pm 1.7	0.7 \pm 0.3	1.5 \pm 0.5	11.8 \pm 1.8	4.0 \pm 0.7	7.9 \pm 2.0	67	
annual	18.2 \pm 2.0	0.9 \pm 0.3	5.4 \pm 1.0	24.5 \pm 2.2	7.1 \pm 0.7	17.4 \pm 2.3	71	
<u>TUP</u>								
summer	4.8 \pm 1.0	<0.1 \pm < 0.1	3.9 \pm 1.0	8.7 \pm 1.4	6.3 \pm 0.5	2.4 \pm 1.5	27	
fall	8.8 \pm 1.5	0.2 \pm 0.2	2.6 \pm 0.7	11.6 \pm 1.6	14.1 \pm 0.9	-2.5 \pm 3.4	-22	
winter	12.6 \pm 2.6	1.6 \pm 1.6	1.9 \pm 0.5	16.1 \pm 3.1	28.4 \pm 1.7	-12.3 \pm 3.5	-76	
spring	42.4 \pm 6.2	6.3 \pm 6.3	3.1 \pm 0.8	51.8 \pm 8.9	68.7 \pm 4.5	-16.9 \pm 9.9	-33	
annual	68.6 \pm 6.9	8.1 \pm 6.5	11.5 \pm 1.6	88.2 \pm 9.6	117.5 \pm 4.9	-29.3 \pm 10.8	-33	

Table 3 (continued)

Phosphorus Form	Input			Output		Retention	
	Stream Flow	Ungauged Flow	Precipitation	Total	Stream Flow	Absolute (In-Out)	Relative %
<u>TP</u>							
summer	6.6 ± 1.0	<0.1 ± <0.1	5.7 ± 0.8	12.3 ± 1.3	6.8 ± 0.5	5.5 ± 1.3	45
fall	10.1 ± 1.5	0.2 ± 0.2	3.8 ± 0.5	14.1 ± 1.6	14.7 ± 0.9	-0.6 ± 1.8	-4
winter	18.0 ± 2.4	1.8 ± 1.6	2.7 ± 0.4	22.5 ± 2.9	30.3 ± 1.7	-7.8 ± 3.4	-34
spring	52.1 ± 5.9	6.9 ± 6.3	4.5 ± 0.6	63.5 ± 8.7	72.7 ± 4.5	-9.2 ± 9.7	-14
annual	86.8 ± 6.6	8.9 ± 6.5	16.7 ± 1.2	112.4 ± 9.3	124.5 ± 4.9	-12.1 ± 10.5	-11

TABLE 4 Harp 4 beaver pond waterborne nitrogen input, output and retention (gN/m²) for the 1987/88 hydrologic year. Shown are estimates \pm 1 SD.

Nitrogen Form	Input				Output		Retention	
	Stream Flow	Ungauged Flow	Precipitation	Total	Stream Flow		Absolute (In-Out)	Relative %
<u>NH₄-N</u>								
	summer	<0.01 \pm < 0.01	0.01	0.07 \pm 0.01	0.08 \pm 0.01	0.01 \pm <0.01	0.07 \pm 0.01	87
	fall	0.03 \pm 0.01	0.01	0.10 \pm 0.01	0.13 \pm 0.01	0.05 \pm 0.01	0.08 \pm 0.02	62
	winter	0.13 \pm 0.02	0.01 \pm 0.01	0.09 \pm 0.01	0.22 \pm 0.02	0.24 \pm 0.03	-0.02 \pm 0.04	-9
	spring	0.18 \pm 0.03	0.01 \pm 0.03	0.10 \pm 0.01	0.29 \pm 0.04	0.48 \pm 0.06	-0.19 \pm 0.07	-66
annual		0.34 \pm 0.03	0.02 \pm 0.03	0.36 \pm 0.02	0.72 \pm 0.05	0.78 \pm 0.06	-0.06 \pm 0.08	-8
<u>NO₃-N</u>								
	summer	<0.01 \pm <0.01	0.01	0.09 \pm 0.01	0.10 \pm 0.01	<0.01 \pm <0.01	0.10 \pm 0.01	100
	fall	0.04 \pm < 0.01	<0.01 \pm <0.01	0.15 \pm 0.02	0.18 \pm 0.02	0.07 \pm 0.01	0.11 \pm 0.02	61
	winter	0.13 \pm 0.01	0.02 \pm 0.01	0.20 \pm 0.02	0.35 \pm 0.03	0.18 \pm 0.01	0.17 \pm 0.03	49
	spring	0.33 \pm 0.03	0.06 \pm 0.07	0.14 \pm 0.02	0.53 \pm 0.07	0.50 \pm 0.04	0.03 \pm 0.08	6
annual		0.50 \pm 0.03	0.08 \pm 0.07	0.58 \pm 0.04	1.16 \pm 0.08	0.75 \pm 0.04	0.41 \pm 0.09	35

Table 4 (continued)

Nitrogen Form	Input				Output Stream Flow	Retention	
	Stream Flow	Ungauged Flow	Precipitation	Total		Absolute (In-Out)	Relative %
<u>TON</u>							
summer	0.06 ± 0.01	0.01	0.06 ± 0.02	0.12 ± 0.02	0.06 ± < 0.01	0.05 ± 0.022	46
fall	0.23 ± 0.03	0.01 ± <0.01	0.02 ± 0.02	0.26 ± 0.03	0.31 ± 0.01	-0.06 ± 0.04	-26
winter	0.41 ± 0.05	0.05 ± 0.05	0.03 ± 0.02	0.49 ± 0.07	0.73 ± 0.04	-0.24 ± 0.08	-50
spring	0.90 ± 0.11	0.12 ± 0.06	0.04 ± 0.02	1.06 ± 0.13	1.34 ± 0.08	-0.28 ± 0.15	-27
annual	1.60 ± 0.13	0.18 ± 0.08	0.15 ± 0.04	1.93 ± 0.15	2.44 ± 0.09	-0.51 ± 0.18	-26
<u>TN</u>							
summer	0.06 ± 0.01	0.01	0.22 ± 0.02	0.28 ± 0.02	0.08 ± <0.01	0.20 ± 0.02	71
fall	0.29 ± 0.03	0.01 ± <0.01	0.26 ± 0.02	0.56 ± 0.04	0.43 ± 0.01	0.13 ± 0.04	23
winter	0.66 ± 0.05	0.07 ± 0.05	0.33 ± 0.03	1.06 ± 0.08	1.15 ± 0.03	-0.09 ± 0.08	-8
spring	1.40 ± 0.11	0.20 ± 0.09	0.28 ± 0.03	1.88 ± 0.14	2.32 ± 0.07	-0.44 ± 0.16	-23
annual	2.41 ± 0.13	0.28 ± 0.10	1.09 ± 0.05	3.78 ± 0.17	3.98 ± 0.08	-0.20 ± 0.19	-5

TABLE 5 Runoff, water retention and phosphorus and nitrogen export and import from Harp beaver pond for the 1987/88 hydrologic year.

	Period						
	Annual 1987/88	Summer & Fall	Winter & Spring	April 1988	April 1-10, 1988	Dec. 10-16, 1987	Jan 31 - Feb 6, 1988
No. Days	365	182	183	30	10	7	7
Runoff (1 x 10 ⁶ L) (% annual)	293	29 (10%)	264 (90%)	132 (45%)	80 (27%)	17 (6%)	13 (4%)
Residence Time (days)	47	242	26	9	5	16	21
<u>Total Phosphorus (g)</u>							
Export	4744	820 (17%)	3924 (83%)	1503 (32%)	846 (18%)	248 (5%)	220 (5%)
Import	4284	1005 (23%)	3280 (77%)	1339 (33%)	-	-	-
<u>Total Nitrogen (Kg)</u>							
Export	151	19 (13%)	132 (87%)	53 (35%)	33 (22%)	9 (6%)	9 (6%)
Import	144	32 (22%)	112 (78%)	41 (29%)	-	-	-

Figure 1

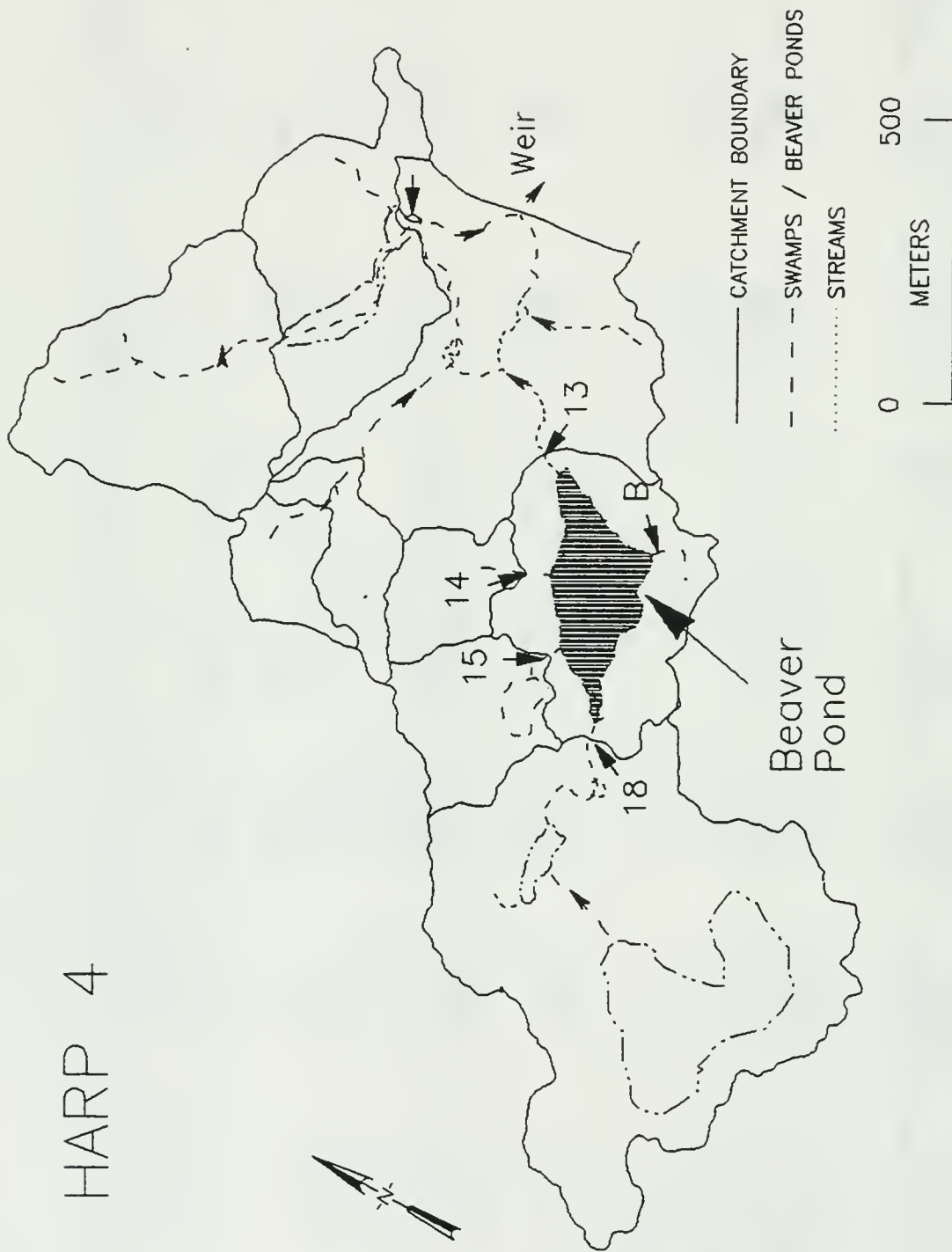


Figure 2

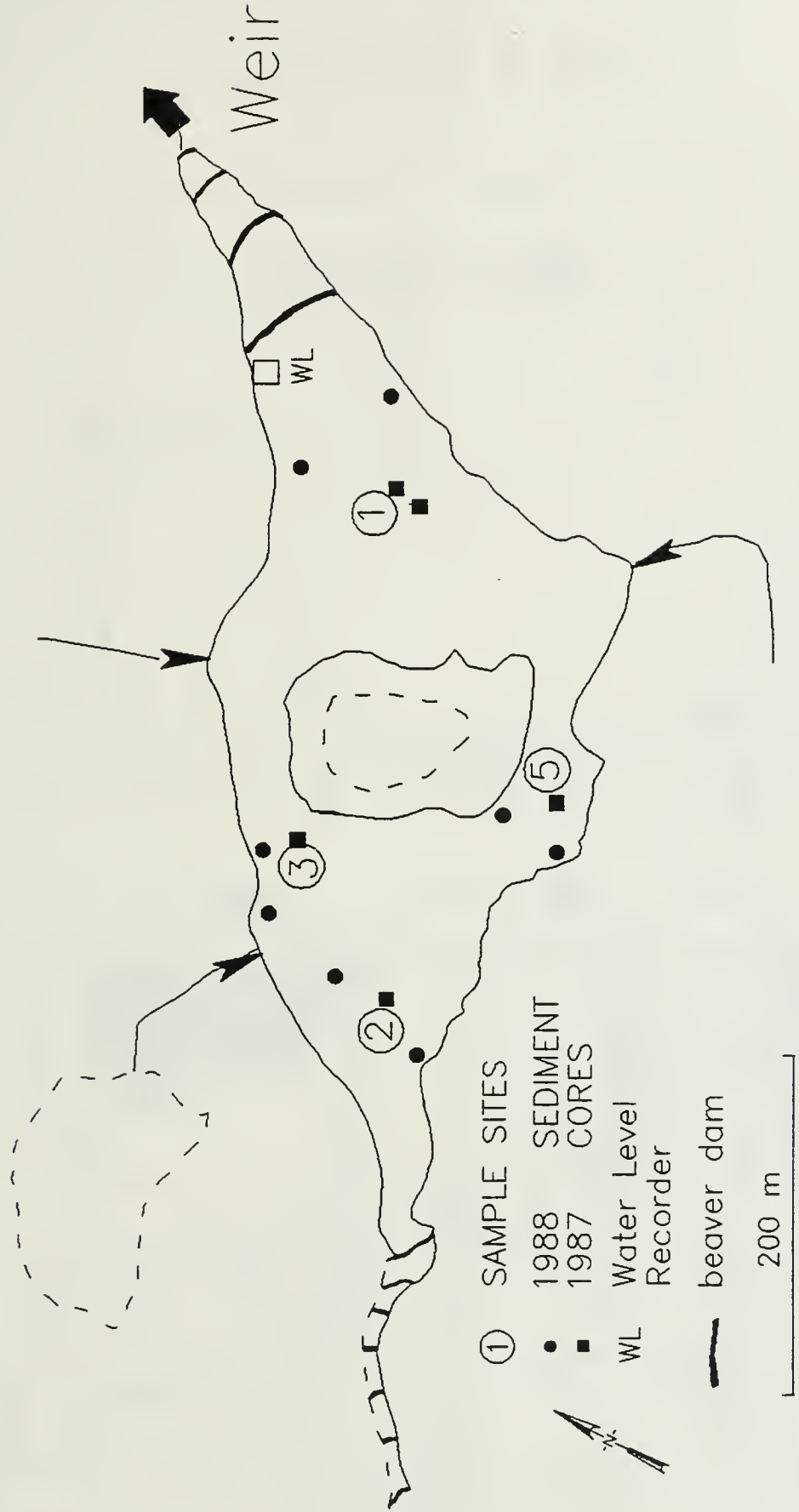
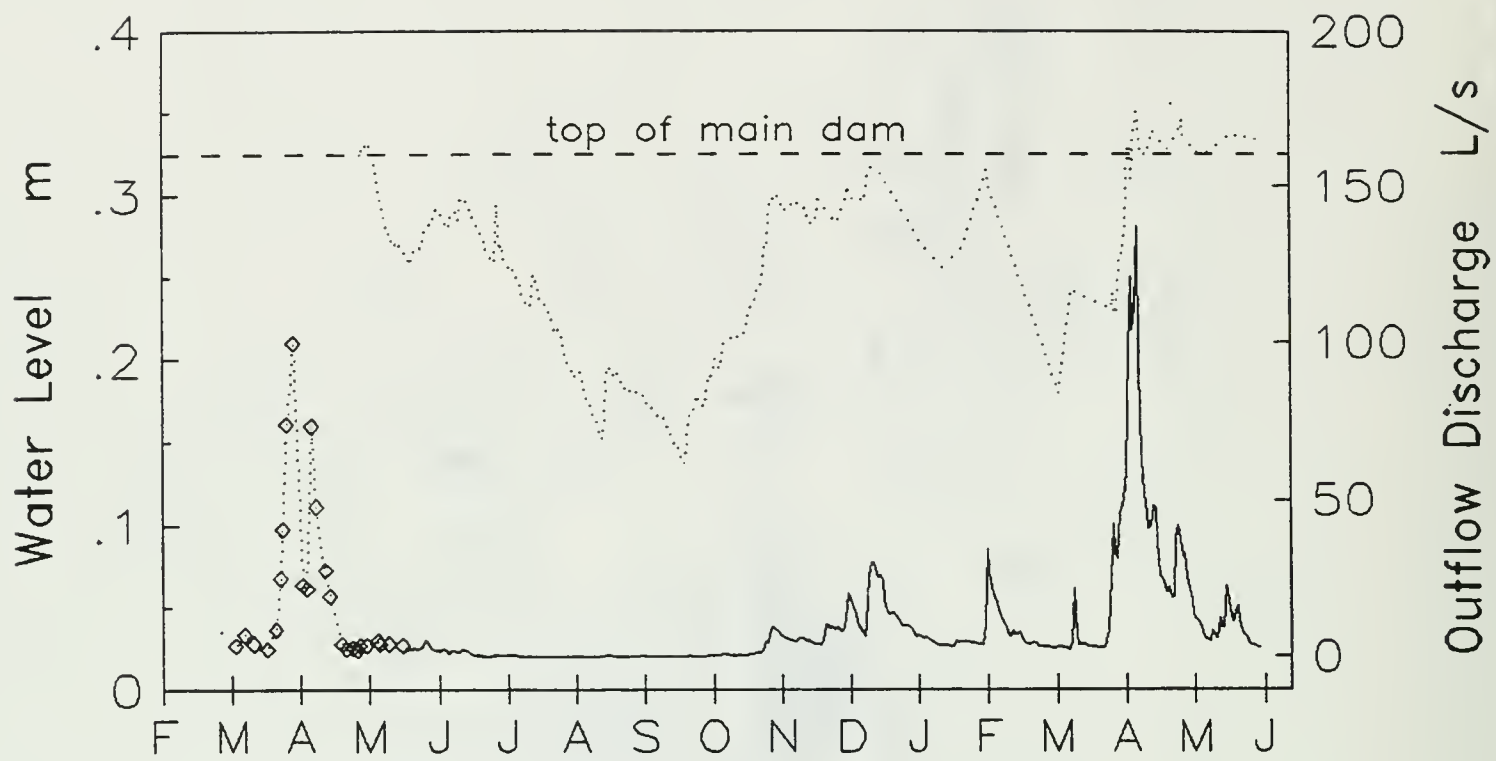


Figure 3

Harp 4 Beaver Pond

a)



b)

⑮ temp oC

ice

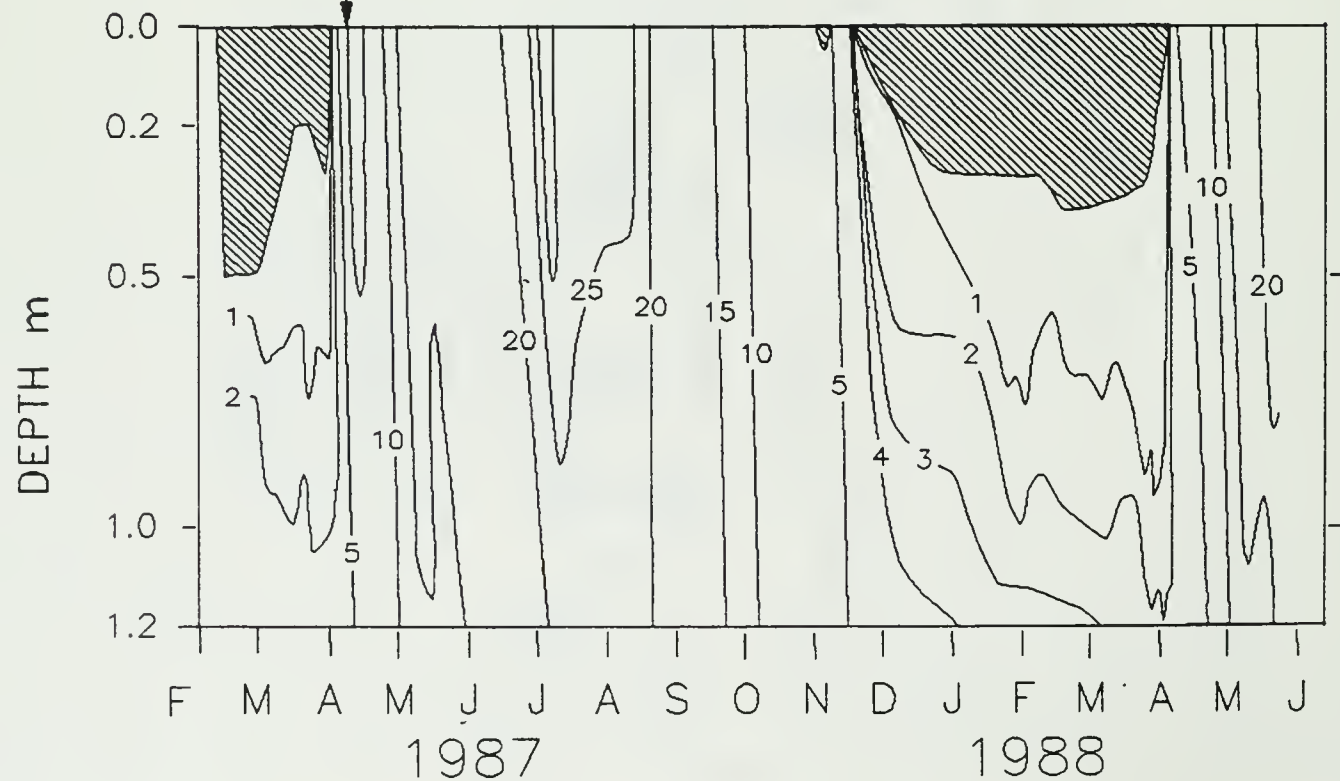


Figure 4

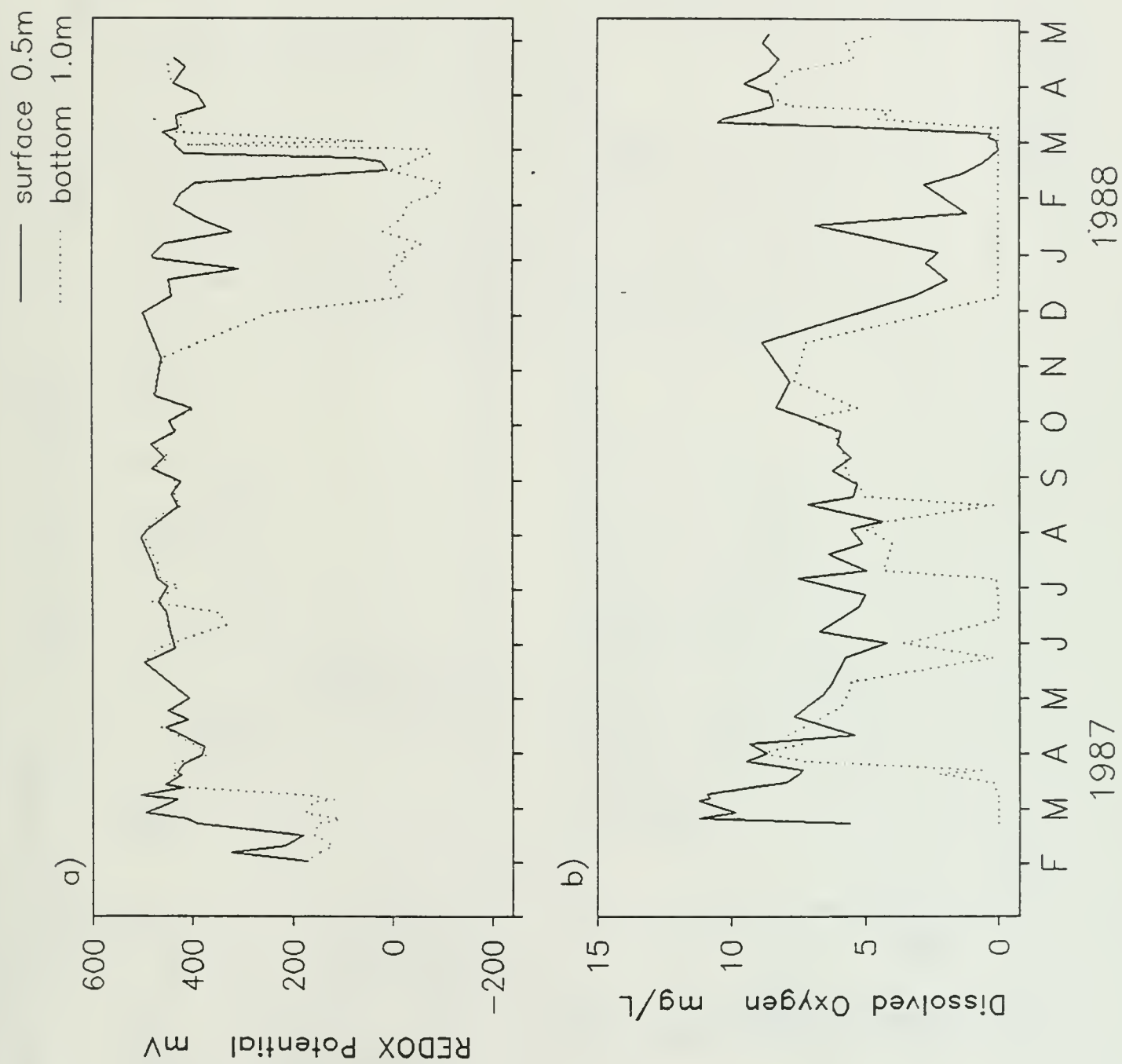


Figure 5

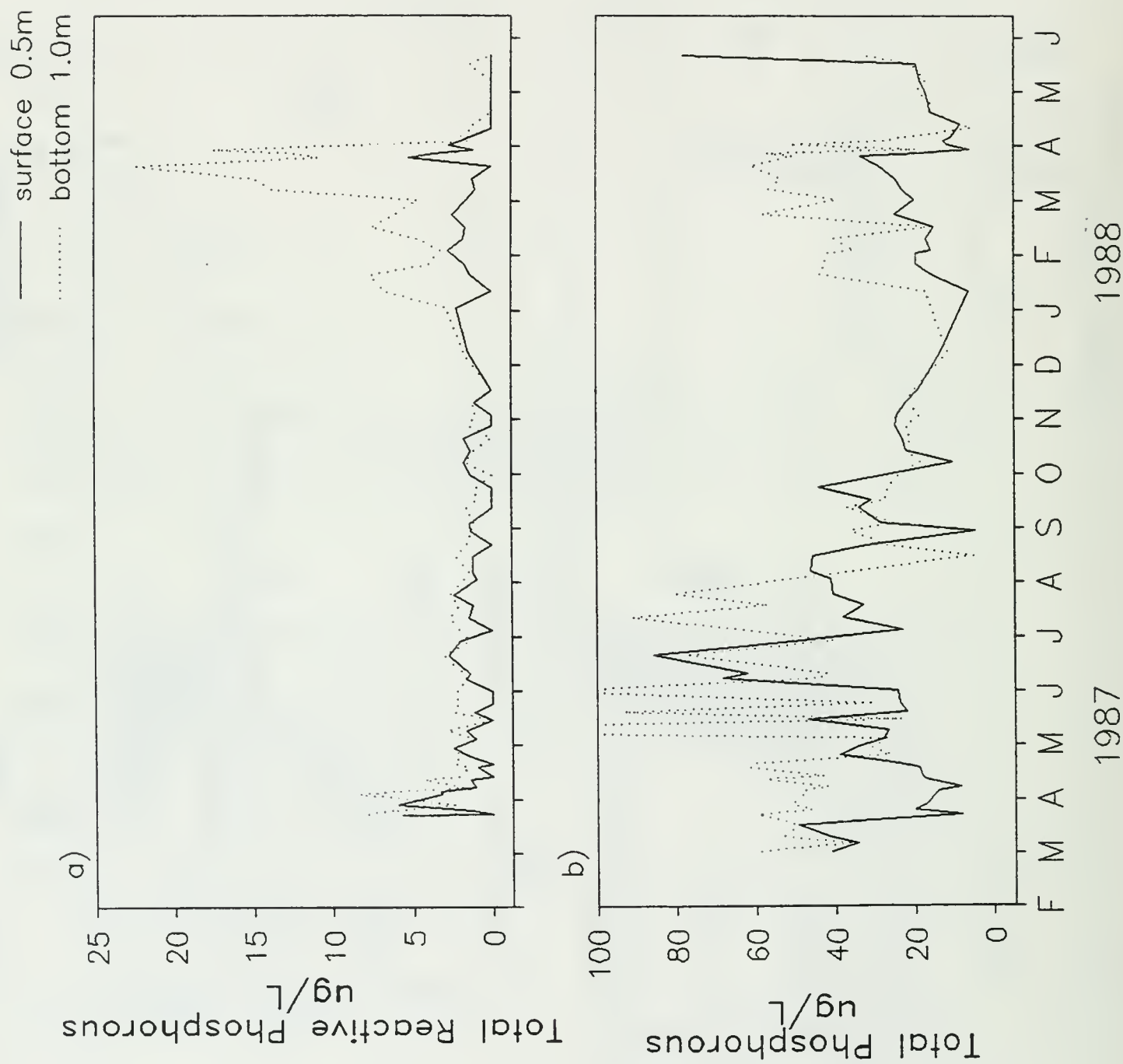


Figure 6

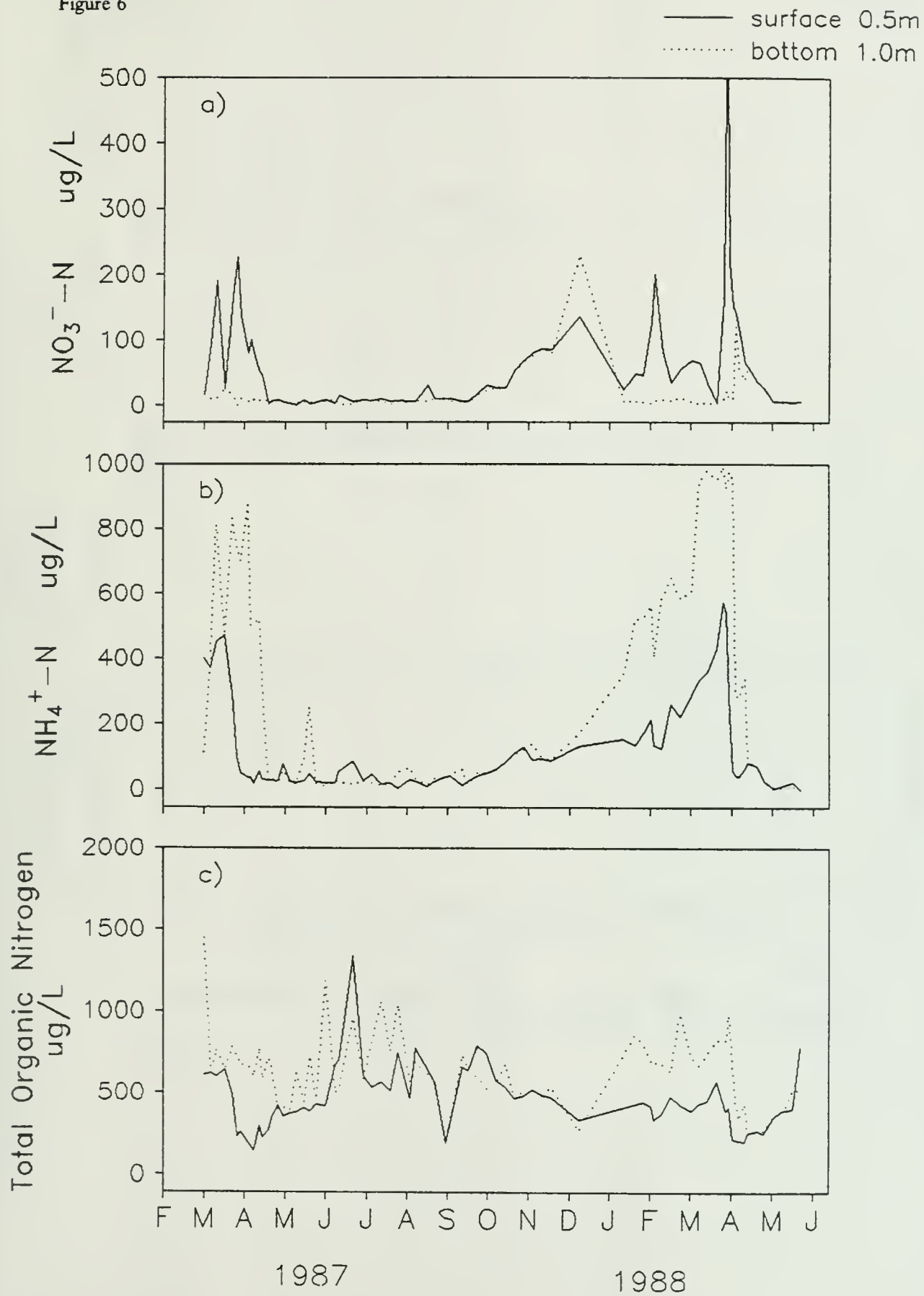


Figure 7

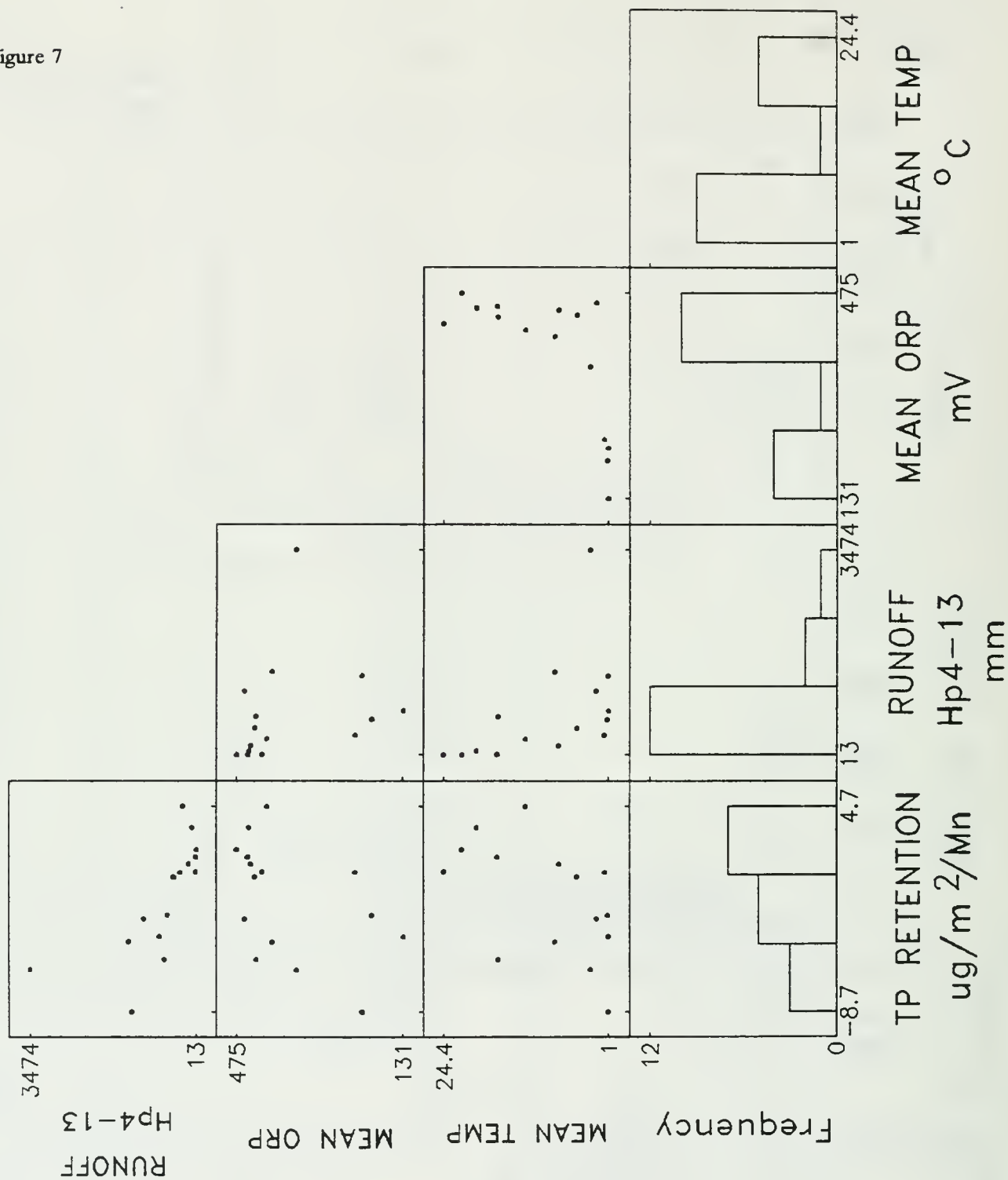


Figure 8

